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FIELD WORK ON THE POPULATION STRUCTURE OF *OENEIS MELISSA SEMIDEA* (*SATYRIDAE*) FROM THE PRESIDENTIAL RANGE, NEW HAMPSHIRE

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INTRODUCTION

The purpose of this study was to assess the extent to which various local populations of *Oeneis melissa semidea* are isolated from one another. This subspecies of a characteristically North American arctic and western alpine species is found throughout the alpine areas of the Presidential Range in New Hampshire, but as has been found with other butterfly species, it seems to have certain localized areas of greatest abundance between which individuals are seldom found. The presence or absence of the butterfly in a given area of the range presumably depends on the presence and quantity of available host food plant, in this case alpine grasses and sedges, and various microclimatic factors such as ground temperature, moisture, and depth of snow cover during the winter.

The study was undertaken with the following two alternative hypotheses as its basis:

1. The population of *Oeneis melissa semidea* is homogeneous over the entire Presidential Range, that is, it is not broken down into local breeding populations, and that a constant flow of individuals and consequently genetic exchange occurs between the various centers of abundance along the range. This situation would tend to result in minimal or at least continuous variation between samples of individuals drawn from selected areas of the range.

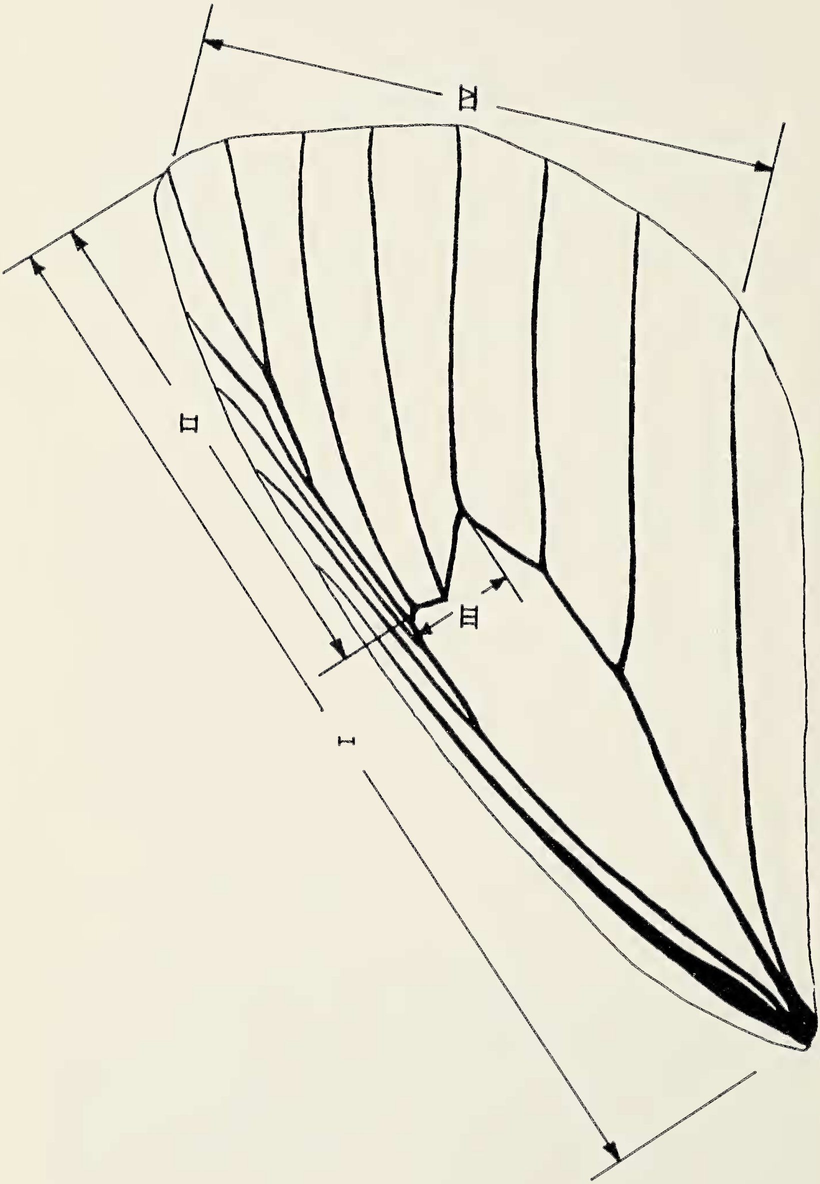

Fig. 1. Diagram of forewing of *Oeneis melissa semidea* showing measurements made in Roman numerals.

2. The population of *Oeneis melissa semidea* is not homogeneous, but rather it is broken down into discrete local breeding populations with little or no exchange of individuals or genetic information between them. This situation would tend to result in greater variation between samples of individuals drawn from selected areas of the range.

It was expected that the true situation for this butterfly lay somewhere between the two hypotheses, depending on certain ecological and environmental factors.

METHODS

The mark-release-recapture method was originally employed to assess the movement of individuals between areas on the range. Individuals were marked with dots of waterproof paint (see Ehrlich, 1960), the position of which identified each individual with a number. In this way, any individual recaptured could be identified as to place of origin, and movements could be detected. In addition, recaptures could be used to estimate the size of the population as a whole, and for individual areas.

Between the dates of 27 June and 7 July, 51 marked individuals were released in the Cowpasture, a rather extensive, relatively flat area at mile 7 of the Mt. Washington auto road. No subsequent recaptures of any of these individuals were made in the Cowpasture or elsewhere. Since difficulty was being encountered in obtaining significant numbers of individuals for marking, and because a number of factors related to the marking technique itself were becoming serious problems, the mark-release-recapture attempts were ended, and pure sampling from the population was begun.

From 8 July until 15 July samples of as large a number of specimens as possible were taken from four selected areas of the Presidentials. From north to south along the range these areas were: Monticello Lawn on Mt. Jefferson (5300-5400 ft.), the area surrounding the Gulf Tanks along the Mt. Washington Cog Railway between the summits of Mt. Washington and Mt. Clay (5700-5900 ft.), the Cowpasture at mile 7 of the Mt. Washington auto road (5700-5800 ft.) and Bigelow Lawn, directly south of the cone of Mt. Washington (5400-5500 ft.). A total of 115 individuals were taken by the author and another 30 were obtained from Donald Lennox of Jefferson, N. H., who collected in the Cowpasture on 8 and 15 July. Of those collected by the author, 13 females were kept alive and later released on

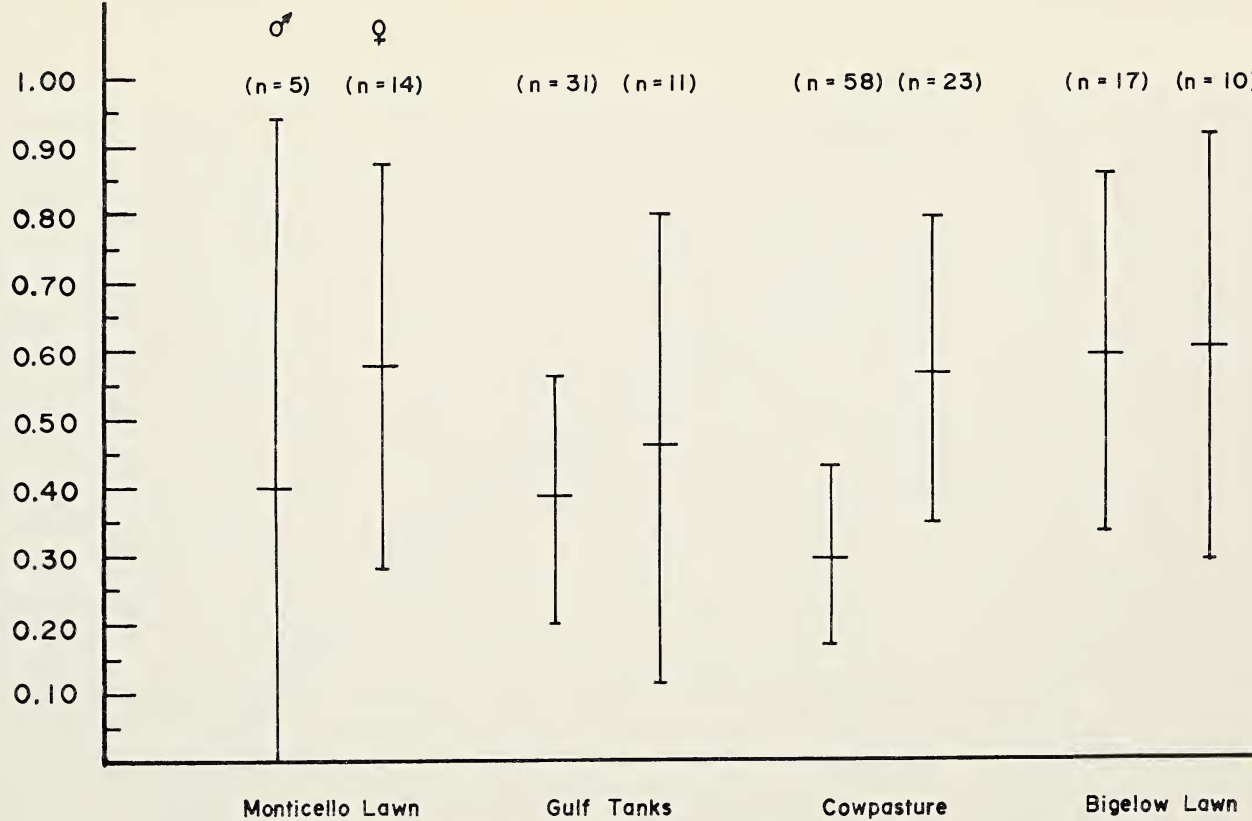

Fig. 2. Frequency of spotting for samples of *Oeneis melissa semidea* from areas of the Presidential Range sampled during the summer of 1969. Observed frequency shown by horizontal dashes; 95% confidence limits shown by vertical lines.

the summit of Mt. Mooselauke at the western edge of the White Mountains. A grant total of 132 individuals were therefore available for study following the initial field work required for the study. Field work ended 2 August.

Up to the present time five characters have been analyzed in an effort to provide evidence of genetic isolation between breeding populations of the butterfly. Males and females have in all cases been treated as separate populations in the analyses because of the lack of any evidence to treat them as the same, and also because the mean values for each character analyzed differ between males and females from a given area, sometimes significantly.

The first character analyzed was the frequency of occurrence of a spot in cell R_5 of the forewing of the butterfly. Determination of the occurrence of a spot was made by visual inspection. In only a small number of cases was the use of a hand lens necessary for determination. The occurrence of a spot was defined as the appearance of a group of scales between veins R_5 and M_1 in the submarginal area of the forewing which were of a darker color (usually black) than the ground color of the wing and which were distinguishable on both the dorsal and ventral surfaces of the wing. This definition eliminated certain color variation appearing most commonly on the forewings of females such as a small light ochreous patch of scales against a darker ground color but without a darker center which is characteristic of eyespots.

The remaining characters were the linear distances between various points on the forewing (see figure 1 for diagram):

I — extreme base of wing to the end of vein R_4 (a standardized indication of the overall length of the wing)

II — base of M_1 to the end of R_4 measured from inside discal cell

III — width of discal cell from base of M_3 to base of R_3

IV — end of 2nd-A to end of R_4 (indication of the width of the wing)

Measurements were made under a 10 X dissecting microscope with a scale accurate to 0.05 mm. This scale was made by photographing a 30 cm. ruler accurate to 0.5. and photographically reducing the image 10 times on printing paper.

RESULTS

Results of the frequency of spotting analysis show a number of interesting trends. First, the observed frequencies of the occurrence of a spot in all cases were higher in female samples

Table 1

Values of "t scores" of comparisons of frequencies of spotting between populations of Oeneis melissa from the Presidential Range, N. H.

males

	Monticello Lawn	Gulf Tanks	Cowpasture	Bigelow Lawn
Monticello Lawn	———	0.058	0.474	0.760
Gulf Tanks		———	0.904	1.37
Cowpasture			———	2.25*
Bigelow Lawn				———

females

	Monticello Lawn	Gulf Tanks	Cowpasture	Bigelow Lawn
Monticello Lawn	———	0.585	0.042	0.024
Gulf Tanks		———	0.610	0.671
Cowpasture			———	0.187
Bigelow Lawn				———

* Significant

than in male samples from a given area. In only one case, that of the Cowpasture samples, was the difference between male and female frequencies significant ($P<0.1$). It is entirely possible that, had sample sizes been larger, a significant degree of difference would have been found between male and female spotting frequencies from the remaining three areas. This is especially true for the Monticello Lawn and the Gulf Tankes areas. Comparisons of male samples showed a significant difference between Bigelow Lawn and Cowpasture ($P<0.025$), and a difference approaching significance between Bigelow Lawn and Gulf Tanks ($P<0.2$). All other comparisons of spotting frequency, including those between female samples, showed no significant differences (table 1; figure 2).

Results of the forewing measurement analyses show that females are larger than males on the average, a result which is almost invariable with most butterfly species (table 2; figure 3). All but the Monticello Lawn samples show that this difference is highly significant for measurements I and II (table 3). Again, small sample sizes from Monticello Lawn may account for this discrepancy. Between samples of a given sex from the four areas very few differences even approaching significance were found (tables 4 and 5). Males, however, tended to show greater differences than did females. Once again, little reliance can be placed on values obtained from the male Monticello Lawn sample because of its extremely small size.

DISCUSSION

The results of this study have been inconclusive. However, the data from the five character analyses combined with field observations can be used to draw at least tentative conclusions until further field work can be undertaken.

From the observations of the butterfly, the hypothesis that the population is divided into discrete local breeding populations is likely, especially between the northern and southern portions of the Presidential Range. Between Mt. Jefferson and Mt. Clay, for example, the ridge drops to below 5000 ft. and enters typical scrub vegetation. It is unlikely that *semidea* would fly this low unless it were blown from higher ground. The butterfly rarely flies more than a foot or two above the surface of the ground, so an individual which might accidentally wander downslope would eventually enter completely foreign vegetation and would probably seek higher ground again. This tendency to seek higher ground, more commonly termed hilltopping, has been recorded

Table 2

Mean values and 95% confidence limits of wing measurements made on samples of Oeneis melissa semidea from the Presidential Range, New Hampshire.

	I	II	III	IV
Monticello Lawn				
male (n=5)	23.9 ± 0.99	10.4 ± 0.37	3.0 ± 0.18	14.6 ± 0.28
female (n=9)	24.4 ± 0.82	10.9 ± 1.5	3.0 ± 1.34	14.5 ± 0.34
Gulf Tanks				
male (n=30)	23.0 ± 0.39	10.1 ± 0.02	2.9 ± 0.09	14.1 ± 0.29
female (n=7)	24.3 ± 0.83	11.1 ± 0.73	3.0 ± 0.25	14.6 ± 0.50
Cowpasture				
male (n=34)	23.2 ± 1.04	9.8 ± 0.59	2.9 ± 0.19	13.9 ± 0.95
female (n=12)	24.4 ± 0.57	10.9 ± 0.31	3.0 ± 0.09	14.4 ± 0.31
Bigelow Lawn				
male (n=20)	23.4 ± 0.42	10.4 ± 0.38	3.0 ± 0.09	14.2 ± 0.34
female (n=9)	24.9 ± 0.97	11.3 ± 0.46	3.1 ± 0.19	14.8 ± 0.59

Table 3

Exact percentages (divided by 100) of "t-scores" of comparisons between male and female samples of Oeneis melissa semidea from designated areas of the Presidential Range, New Hampshire.

	ML	GT	C	BL
I	0.608	0.00505**	0.00069**	0.0015**
II	0.120	0.0006**	0.000**	0.0062**
III	1.000	0.326	0.080	0.243
IV	0.684	0.096	0.062	0.055

* significant ($P < 0.05$)
** highly significant ($P < 0.01$)

for many species of butterflies (for review see Shields, 1967) including *Oeneis melissa* (Munroe, 1948 (1951); Anthony, 1969). In the far north and the Rocky Mountains, *Oeneis melissa* flies only above or north of the scrub line. On Mt. Washington and the surrounding peaks of the Presidential Range the only individuals which actively fly appreciable distances are males in search of females. Since the females almost invariably remain in areas where grasses and sedges are the dominant form of vegetation, males tend to congregate in these areas also. Thus, between Mt. Jefferson and Mt. Clay a partial barrier to movement of individuals and genetic exchange exists.

On Mt. Washington itself one interesting relationship seems evident between the three sampled areas. Looking at the t scores for spotting frequency computed between the samples from each of the three areas, the significance of the differences between the samples appears to be almost directly related to their directions from each other relative to the direction of the prevailing wind from the west. Between the Gulf Tanks and the Cowpasture there is more than a 25% chance that the populations have the same frequency of spotting. This is reasonable since the Cowpasture is in the direct path of the prevailing wind from the Gulf Tanks. An individual could be and frequently probably is blown from the Gulf Tanks area into the Cowpasture in a matter of minutes. On the other hand, between the Gulf Tanks area and Bigelow Lawn there is only about a 15% chance that the populations have the same frequency of spotting. Again the directions of Bigelow Lawn from the Gulf Tanks relative to the direction of the prevailing wind would account for the reduced chances that the populations have the same frequency. Finally, between the Cowpasture and Bigelow Lawn there is almost no chance, less than 2%, that the populations have the same frequency of spotting. This is because there is almost no chance that an individual could be blown from one to the other, since a line between them is practically perpendicular to the direction of the prevailing winds. Individuals which are blown anywhere are probably blown directly east or southeast, in the case of the Cowpasture into the Great Gulf or Huntington Ravine, and in the case of Bigelow Lawn into Tuckerman's Ravine or the Gulf of Slides. In addition, the Alpine Garden, which lies directly between the Cowpasture and Bigelow Lawn, is surprisingly devoid of the butterfly, even though in the past it has been regarded as a prime collecting area for *Oeneis melissa.*

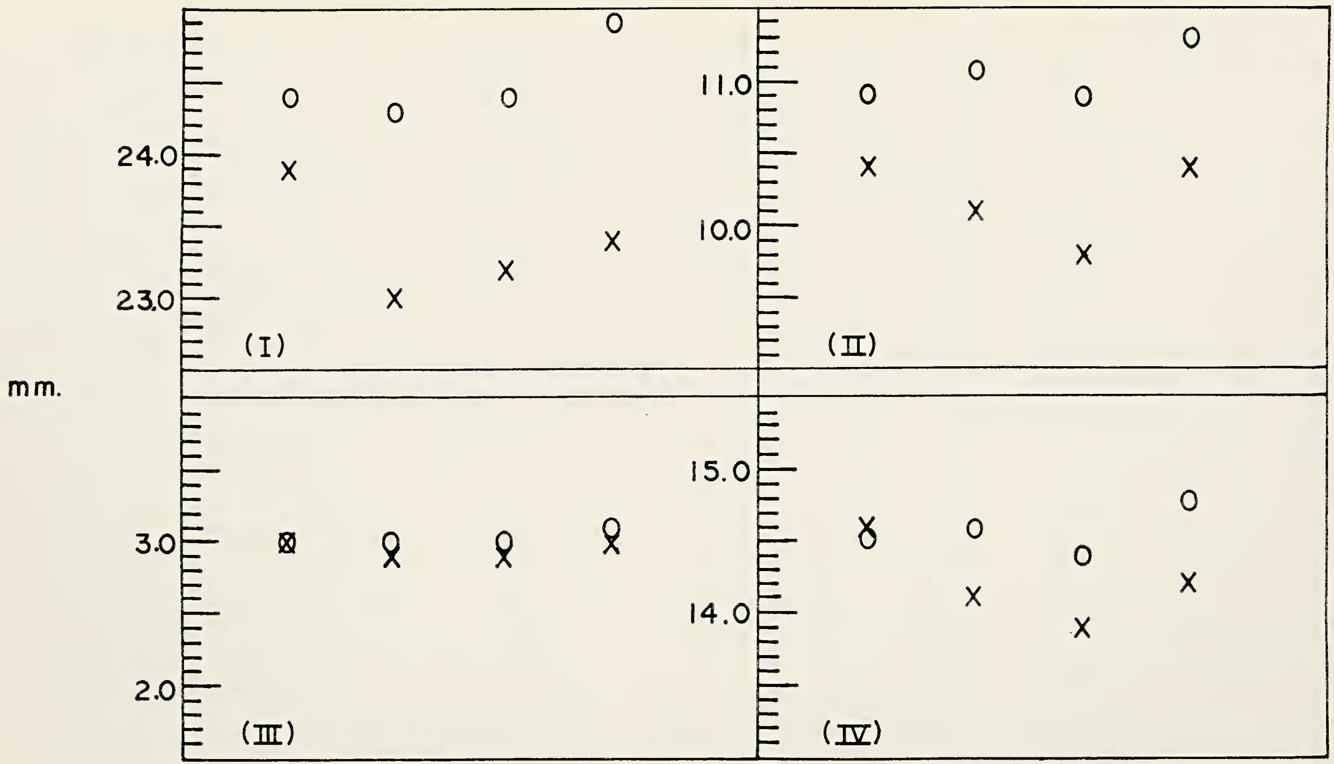

Fig. 3: Diagram of values of measurements made on the forewings of *Oeneis melissa semidea* from the Presidential Range, N. H. Roman numerals correspond to those of fig. 1. ML = Monticello Lawn, GT = Gulf Tanks, C = Cowpasture, BL = Bigelow Lawn.

Table 4

Exact percentages (divided by 100) of "t-scores" of comparisons of wing measurements made on samples of Oeneis melissa semidea from the Presidential Range, New Hampshire.

Males

	ML	GT	C	BL	Measurement
ML	*---	0.078	0.199	0.283	(1)
	---	0.249	0.038*	1.000	(11)
	---	0.062	0.301	1.000	(111)
	---	0.159	0.126	0.251	(1v)
GT		---	0.567	0.126	
		---	0.030*	0.122	
		---	1.000	0.115	
		---	0.323	0.652	
C			---	0.543	
			---	0.002**	
			---	0.050*	
			---	0.164	
BL				---	

				---	

* significant
** highly significant

Table 5

Exact percentages (divided by 100) of "t-scores" of comparisons of wing measurements made on samples of <u>Oeneis melissa semidea</u> from the Presidential Range, New Hampshire.

Females

	ML	GT	C	BL	Measurement
ML	---	0.840	1.000	0.622	(I)
	---	0.586	1.000	0.175	(II)
	---	1.000	1.000	0.657	(III)
	---	0.709	0.748	0.639	(IV)
GT		---	0.814	0.308	(V)
		---	0.506	0.577	(VI)
		---	1.000	0.537	(VII)
		---	0.575	0.589	(VIII)
C			---	0.298	(IX)
			---	0.100	(X)
			---	0.268	(XI)
			---	0.172	(XII)
BL				---	(XIII)
				---	(XIV)
				---	(XV)
				---	(XVI)

Two points mus be emphasized in defense of this attractive relationship. First, the period of time during which this butterfly flies during the summer is short, beginning slightly before the first of July with very small numbers of individuals, reaching a peak in numbers by the end of the second week of July, and ending by the last week in July or the first of August, depending on the weather conditions for a given season. This year (1969), the flight period was probably effectively ended by the 22nd of July because of extremely bad weather which began on that date. By the 2nd of August, when the harsh weather had ended, no butterflies were seen anywhere. Since the flight period of the butterfly is therefore so limited, the period during which genetic exchange between local populations is possible is limited as well. Secondly, during this short flight period the number of days during which adults fly is limited by the weather. The butterfly tends to fly in appreciable numbers only on relatively warm, sunny days, which are few and far between in this above tree-line area of the White Mountains. The butterfly generally will not fly in winds above 40 mph., in temperatures below 45 degrees F., or in fog or rain, unless it is disturbed. Since the butterfly then only flies during relatively "good" weather, and since the wind rarely blows from directions other than the west or northwest during such "good" weather, the chance of movement of individuals by wind action alone in any direction other than from west to east is slight.

A number of inconsistancies exist in the data and field observations of *Oeneis melissa semidea.* First of all, comparisons of frequency of spotting made between areas are not paralleled by the comparisons of wing measurements. In fact, the lack of a definite pattern to the comparisons of the wing measurements casts doubt on the validity of these measurements as genetically controlled characters. The fact that many species of *Oeneis* possess a spot in exactly the same area of the wing that certain individuals of *semidea* do would seem to indicate that spotting is indeed genetically controlled and not subject to differences in time of eclosure, nutritional factors, or other environmental conditions. However, overall size of the butterfly, reflected in the measurements, may indeed be influenced by the above factors. Breeding experiments should resolve this question if a successful technique for raising the butterfly can be developed.

Another inconsistency is found in comparing male and female spotting frequencies from a given area and between areas, and at the same time recalling that the females of this species are more

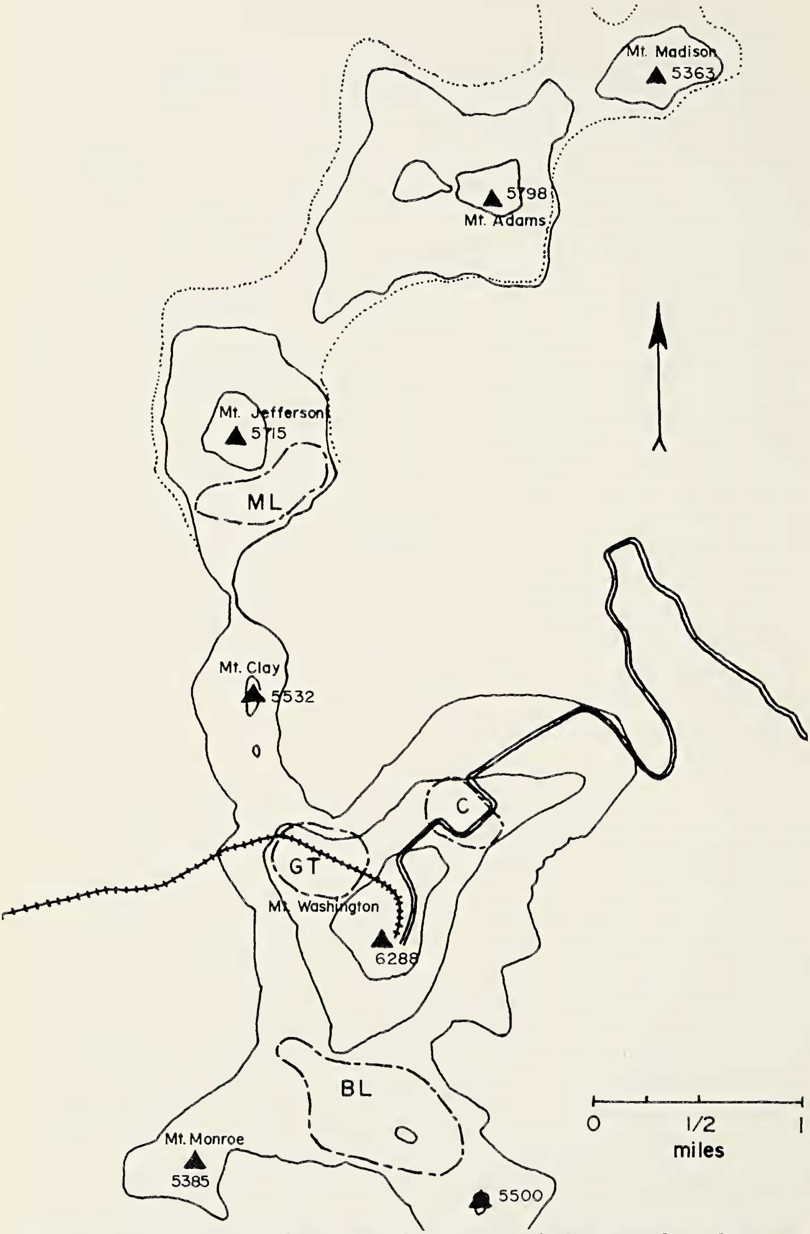

Fig. 4. Map showing above tree line areas of the Presidential Range, New Hampshire.

Areas sampled for *Oeneis melissa semidea* indicated by large capital letters, inclosed by dashed line. ML = Monticello Lawn, GT = Gulf Tanks, C = Cowpasture, BL = Bigelow Lawn.

or less sedentary, whereas the males tend to wander. In this case the question arises as to why the female spotting frequencies are statisically constant and do not at least parallel the males. The only explanation for this that so far appears to be tenable is that the males, because they fly more often and for greater distances are therefore more exposed than the females and are consequently subject to some unknown selective pressure more than are the females. This selection pressure may be resulting in more variation in the male populations than in the female. An interesting point to mention is that there seems to be a slight correlation between the presence of a spot on a given individual and the distinctness of the dark median band on the ventral surface of the hindwing. If indeed there is a correlation between these two characters, then a basis can be laid for suspicion of predatory pressure favoring spotted individuals through selection for a distinct band. It has been proposed that the white band which crosses the wings of certain species of *Limenitis* butterflies produces a form of disruptive coloration, breaking up the outline of the wing and rendering it less easily seen by a potential predator (Platt and Brower, 1968). It seems possible that adult *semidea* are under selective pressure from predators such as certain species of birds which frequent the alpine areas of the Presidentials, and that the distinctness of the median band of the hindwing (which is exposed when males sun themselves on rocks) and likewise the presence of a spot on the forewing is being influenced by this pressure. It is also interesting to note that another species of *Oeneis*, namely *polyxenes*, is found in a very similar arctic relict environment on Mt. Katahdin in Maine. All individuals of this population possess a spot in exactly the same area of the forewing and all are rather invariably distinctly banded. *Oeneis melissa* from the Presidentials, on the other hand, vary considerably in not only the presence but the overall development of a spot as well as in the distinctness of the median band. Unfortunately, no objective means could be devised for determining whether or not a band is distinct, and hence the correlation between band and spot has yet to be statistically shown.

SUMMARY AND CONCLUSIONS

Oeneis melissa semidea from the Presidential Range of New Hampshire was studied in the field, and samples from four areas of the range were taken in an effort to determine the popula-

tion structure of the butterfly. Statisical treatment of five characters yielded no conclusive evidence for either total isolation or lack of isolation between the populations inhabiting the four areas, but field observaton combined with the statistics derived from the frequency of the occurrence of a spot on the forewing of the butterfly indicate that at least partial barriers probably exist between the sampling areas. Movement of individuals between any of the areas was not seen while in the field. Movement by action of the prevailing wind from the west is discussed and cited as probably the major contributor to the breakdown of any spatial or environmental barriers which do exist.

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